

Ethology of the cricket *Endecous (Endecous) chape* Souza-Dias & de Mello, 2017 (Orthoptera: Grylloidea: Phalangopsidae) I: Agonistic and reproductive behavior

MARCOS FIANCO¹, PEDRO GUILHERME BARRIOS DE SOUZA-DIAS², FERNANDO DE FARIAS-MARTINS³, SUZANA MAGRO³, VICTOR MATEUS PRASNIEWSKI³, JÉSSICA RICCI³, EDISON ZEFA⁴, NEUCIR SZINWELSKI³

¹ Programa de Pós-Graduação em Biodiversidade Neotropical, Instituto Latino-Americano de Ciências da Vida e da Natureza, Universidade Federal da Integração Latino-Americana, Av. Tarquínio Joslim dos Anjos n. 1000, Foz do Iguaçu, PR, Brazil.

² Departamento de Entomologia, Museu Nacional, Universidade Federal do Rio de Janeiro, Quinta da Boa Vista, s/n, 20940-040, São Cristóvão, RJ, Brazil.

³ Laboratório de Orthoptera, Centro de Ciências Biológicas e da Saúde, Universidade Estadual do Oeste do Paraná, rua Universitária, n. 2069, Cascavel, PR, Brazil.

⁴ Departamento de Zoologia e Genética, Instituto de Biologia, Universidade Federal de Pelotas, Campus Universitário Capão do Leão s/n, Capão do Leão, RS, Brazil.

Corresponding author: Marcos Fianco (marcos.fianco@hotmail.com)

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Abstract

The mating behaviors of crickets, especially those related to agonistic encounters and oviposition, are poorly known. For example, only 10 of the 1005 valid species of Phalangopsidae have been studied to some extent. Here, we describe the reproductive behavior of *Endecous (Endecous) chape*, characterizing the actions involved in agonistic encounters, mating behaviors (female attraction, pair-formation, courtship, mating, and post-copulatory behavior), and oviposition. We recorded and timed agonistic, mating, and oviposition behaviors in staged trials. The male-male interactions of *E. chape* ranged in aggressiveness from low intensity (only antennal interaction) to high intensity (reciprocal fights). In the mating behavior, males courted females through antennation of the females' abdomen and cerci, followed by production of acoustic signals (with the exception of two males). Copulation occurred with females positioned above males (as is typical of Phalangopsidae), with an average elapsed time of 684.13 s, which is shorter than in other Phalangopsidae. We observed oviposition behavior only when three gravid females were placed together in an arena. Here, we contribute new knowledge of phalangopsid cricket behavior and provide useful information for understanding the evolution of reproductive behaviors. New characters described here can be used in phylogenetic analysis and for future studies about sexual selection and natural history.

Key words

aggressiveness, ethology, Luzarinae, mating behavior, Parque Nacional do Iguaçu

Introduction

From a behavioral viewpoint, crickets (Orthoptera: Grylloidea) use all the main classes of sensory perception for intraspe-

cific communication (chemical, acoustic, tactile, and visual), and present specialized aggressive and hierarchical behaviors as well as a high degree of territoriality when compared to other non-social invertebrates (Alexander 1962). Male-male agonistic behavior, for example, is primarily related to territoriality, and dominance is established through antennal contact, stridulation, and fights (Alexander 1961, Khazraie and Campan 1997, Prado 2006, Wilson et al. 2010). Cricket reproductive behavior includes female attraction by means of the calling song and sexual recognition by antennation (Hardy and Shaw 1983, Balakrishnan and Pollack 1997), which triggers courtship and copulation (Alexander 1966, Alexander and Otte 1967, Alexander 1975, Otte and Cade 1976, Otte 1992, Kortet and Hedrick 2005).

During courtship, males communicate with females through stridulation (Alexander 1966, Zefa et al. 2008), antennation (Prado 2006, Funk 2016), and body vibration (Bell 1980, Zefa et al. 2008, Souza-Dias et al. 2015). Copulation begins when a male inserts his spermatophore duct into the female copulatory papilla for sperm transfer (Alexander and Otte 1967). Post-copulatory behavior includes ingestion of the spermatophore by males (Zefa et al. 2008) or females (Alexander and Otte 1967, deCarvalho and Shaw 2010), and male guarding to prevent the female from either removing the spermatophore or mating with other males (Alexander and Otte 1967, de Mello 2007). For oviposition, females select a suitable oviposition site (Evans 1983) using visual and olfactory cues (Huber et al. 1989, Sugawara 1993).

Although the main points of Grylloidea agonistic and reproductive behavior have been extensively studied in the last decades (Alexander and Otte 1967, Bell 1980, Evans 1988, de Mello and dos Reis 1994, Prado 2006, Funk 2016, Lunichkin et al. 2016), few

studies have focused on the family Phalangopsidae. To date, 10 of the 1005 species of Phalangopsidae have had their reproductive behavior described (Alexander and Otte 1967, Dambach and Lichtenstein 1978, Boake 1984, de Mello and dos Reis 1994, Nischk and Otte 2000, Gnaspini and Pelegatti-Franco 2002, Prado 2006, Zefa et al. 2008, Souza-Dias et al. 2015, Lunichkin et al. 2016), and only three species have had their agonistic behavior studied (Boake 1984, de Mello and dos Reis 1994, Prado 2006). This diversity in the behavioral repertoire is likely to be expanded when other species have been studied, particularly since Phalangopsidae are widely distributed, occupying different strata of tropical and subtropical forests, litter, rock crevices, and caves (Desutter-Grandcolas 1995, Bolfarini and Bichuette 2015, Souza-Dias et al. 2017, Cigliano et al. 2018), and also have diverse morphological variation in structures related to reproduction (Prado 2006, de Mello 2007, Zefa et al. 2008, Lunichkin et al. 2016).

Even with few species studied, the Phalangopsidae present a wide behavioral repertoire among the crickets. For example, males of *Nemoricantor maya* (Hubbell, 1938) produce courtship songs that simultaneously keep the female close and intimidate competing males (Boake and Capranica 1982, Boake 1984). In *Phaeophilacris spectrum* (Saussure, 1878), males and females do not have tympana, so communication during courtship occurs by movement of the air produced by the tegmina of males (Heinzel and Dambach 1987). However, females of *Vanzoliniella sambophila* de Mello & Cezar dos Reis, 1994, do not copulate if the male does not drum the substrate with his forelegs (de Mello and dos Reis 1994). Furthermore, males of *Eidmanacris corumbatai* Desutter-Grandcolas, 1995, have metanotal glands that produce secretions offered as nuptial gifts to females during mating (Prado 2006).

Within the Phalangopsidae, *Endecous* is an exclusively Neotropical genus, and is one of the most diverse genera of Luzarinae. The genus includes three subgenera and 18 species, all of which inhabit leaf litter associated with rock gullies, burrows, caves, and any natural cavities (Souza-Dias et al. 2014, Zefa et al. 2014, Bolfarini and Bichuette 2015, Souza-Dias et al. 2017). These crickets are generalists, have cavicolous and straminicolous populations, and, so far, three troglobitic species have been recognized (Souza-Dias et al. 2017). Recently we collected and described the cricket *Endecous* (*Endecous*) *chape* Souza-Dias & de Mello, 2017, which is abundant in the leaf litter of the Atlantic Forest of Western Paraná and Santa Catarina States, southern Brazil (Souza-Dias et al. 2017). Here, we describe the agonistic (male-male interactions) and reproductive (male-female interaction) behaviors of this cricket, highlighting pair-formation, courtship, post-copulatory, and oviposition behaviors.

Methods

Study area and sampling methods.—Nymphs and adults of *Endecous chape* were sampled in the Parque Nacional do Iguaçu (Iguaçu National Park), Foz do Iguaçu municipality, Paraná state, Brazil, between November 2015 and March 2016. The Iguaçu National Park is one of the largest fragments of Atlantic Forest protected in Brazil, and the largest conservation unit that protects the Atlantic Semideciduous Forest (a phytogeography of the Atlantic Forest). Moreover, the Iguaçu National Park protects areas with Ombrophylous Mist Forest (Araucaria forest) and is considered a world heritage site by UNESCO (UNESCO 1986). The regional climate lies within humid subtropical mesothermal, with a mean annual temperature and rainfall of 19°C and 1600 mm, respectively (Guimarães et al. 2003).

Specimens (23 adults and 76 nymphs) were collected using nocturnal active searching on the Iguaçu National Park trails – Cataratas main trail (25°41.013'S, 54°26.385'W) and Poço Preto trail (25°37.735'S, 54°27.831'W). The national authorization for collection was issued by the Instituto Chico Mendes de Conservação da Biodiversidade ICMBio (SISBio 46964). The species studied is not considered endangered or protected.

Individuals were isolated in circular plastic vials (10 cm height and 15 cm diameter), with paper filter as substrate. Water, in open dishes (0.5 cm height and 2 cm diameter) filled with cotton, and food (fish food flakes) were offered *ad libitum*. We also reared nymphs to adulthood in these conditions. Specimens were acclimated for at least 15 days in an acclimatized room at 23°C, 75% relative humidity, and a 12:12h light/dark photoperiod before experiments.

Laboratory trials.—To observe agonistic encounters and mating behaviors, adult crickets were randomly paired (male-male or male-female) in clear glass arena boxes (20 cm length, 15 cm width, and 15 cm height) with filter paper substrate. For all encounters we used different individuals so that each individual contributed only to a single set of observations. Individuals were placed on opposite sides of the arena, isolated under plastic tea cups for 2 min, with simultaneous cup removal. After observations were completed for each encounter, the arena was cleaned with 98° ethanol and dried for 15 min to eliminate odors, and the filter paper substrate was replaced. All encounters were recorded with a digital camera (Canon® PowerShot SX210) at a resolution of 1280x720 at 30 frames per second.

For the observations of male-male interactions, we staged 25 encounters between pairs of males with all behaviors observed and recorded during 15 min. For mating behavior observations, we staged 22 encounters between 44 randomly selected male-female pairs. We included in our analysis only the encounters that resulted in copulation ($n = 15$ of 22). Since behavior in captivity may not predict natural behavior under field conditions (Fisher et al. 2015), observations were interrupted five minutes after they began if no courtship behavior was observed. For the same reason, after courtship began we waited 15 min from the beginning of copulation. If there was no copulation, observations were interrupted. Observations continued for 20 min after the copulations to verify post-copulatory behavior.

Oviposition behavior was observed for 15 copulated females. Trios of females were placed in the glass arena with wet sand as substrate. This combination was used because in previous observations with one ($n = 5$) or two females ($n = 4$), they did not oviposit. Oviposition behavior was observed for 60 min for one of the three females. After oviposition, we removed the sand from the arena and counted the eggs by sifting through the sand.

All individuals used in our experiments were fixed in undiluted ethanol fuel (Szinwelski et al. 2012, Szinwelski et al. 2013) and deposited in the Laboratório de Orthoptera of Universidade Estadual do Oeste do Paraná (Unioeste).

Behavioral analysis.—We timed the repertoire of behavioral elements (e.g. stridulation, antennation, copulation, and fights) during each behavioral unit (agonistic encounters, mating behaviors, and oviposition) that comprised *E. chape* agonistic and reproductive behavior. We report means, standard deviations and ranges for all behavioral elements observed, as well as the number of oviposited eggs. Based on these estimates, we created an ethogram which describes the sequence of mating behaviors.

Results

Male-male interactions.—After removing the tea cups, males remained almost motionless for $35.62 \text{ s} \pm 12.04$ (11 – 64 s, $n = 25$) and then began to pass their antennae and foreleg tarsi over their mouth parts (grooming behavior). Males then walked through the arena touching the substrate with their antennae. The first contact between males was by antennation in a face-to-face position (Fig. 1A), followed by antennal lashing. This behavior and face-to-face position occurred in all interactions and before any other behavior.

After antennation, we observed a sequence of aggressive behaviors and a sequence of same-sex sexual behavior (Bailey and Zuk 2009). From the least to the most aggressive, the behaviors observed were: (i) males remaining immobile or with few movements throughout the arena, without contact ($n = 12$); (ii) antennal contact with emission of song by one male (Fig. 1B) while the other male (subordinate) went to the corner and the dominant remained in the center ($n = 2$); (iii) antennal contact followed by reciprocal fight with subsequent escape of one male while the other male remained in the center of the arena making slight movements ($n = 4$); (iv) the same behavior presented in (iii), plus song emitted by the winning male in the center of the arena ($n = 4$) (Fig. 1D). We observed same-sex sexual behavior in three pairs, characterized by: reciprocal “courtship” with males touching each other with antennae and forelegs, as observed in a male-female courtship, followed by partial exposure of the genitalia and spermatophore production (Fig. 1C). In two of these cases we did not observe fights or escape ($n = 2$), but in one case, after exposing the spermatophores, both males fought and emitted songs, followed by one male retreating to the corner of the arena.

Except for the first behavior (i), all males lifted their bodies a few times during observations. All fights were brief ($8.37 \text{ s} \pm 2.72$

(4 – 15 s, $n = 8$)), mutual, and consisted of fast hindleg kicks, bites, and tarsal pushes. Songs were emitted with the tegmina lifted around 80° in relation to the body axis. When male/male courtship occurred, all males lifted their abdomen and moved the cerci and forelegs. The dominant males were those which remained in the center of the arena, walking and touching the substrate with their antennae while the subordinate male was at the corner, almost motionless.

Mating behavior.—After starting the experiment, both male and female walked through the arena touching the substrate with antennae and maxillary palpi. Males scavenged the substrate more actively than females ($91.73 \text{ s} \pm 97.4$ (3 – 427 s, $n = 15$) and $29.86 \text{ s} \pm 23.2$ (0 – 72 s, $n = 15$), respectively). While scavenging the substrate, both repeatedly passed their antennae and foreleg tarsi over their labial and maxillary palpi, labrum, clypeus, and mandibles, as well as rubbed their hindleg tarsi against the cerci (grooming). The first contact between male and female occurred through mutual antennation on any body part while making rapid movements of the antennae. The elapsed time until first antennal contact was $119.86 \text{ s} \pm 164.31$ (7 – 651 s, $n = 15$), and antennation between them lasted $17.46 \text{ s} \pm 19.37$ (3 – 68 s, $n = 15$).

After antennal contact, 13 of 15 males initiated courtship by placing themselves next to the female (Fig. 2A) and touching her tergites, ovipositor, or cerci with their antennae or forelegs. At the same time, males elevated their tegmina about 80° in relation to their horizontal axis (Fig. 2B) and emitted intermittent acoustic signals. Two males did not produce acoustic signals and immediately assumed the mating position after antennation. When acoustic signals were produced, females touched male cerci or tergites with her antennae, sometimes kicking the male’s antennae and body with her hindleg, while males stridulated intermittently. During this time, the male slowly neared the female and performed a series

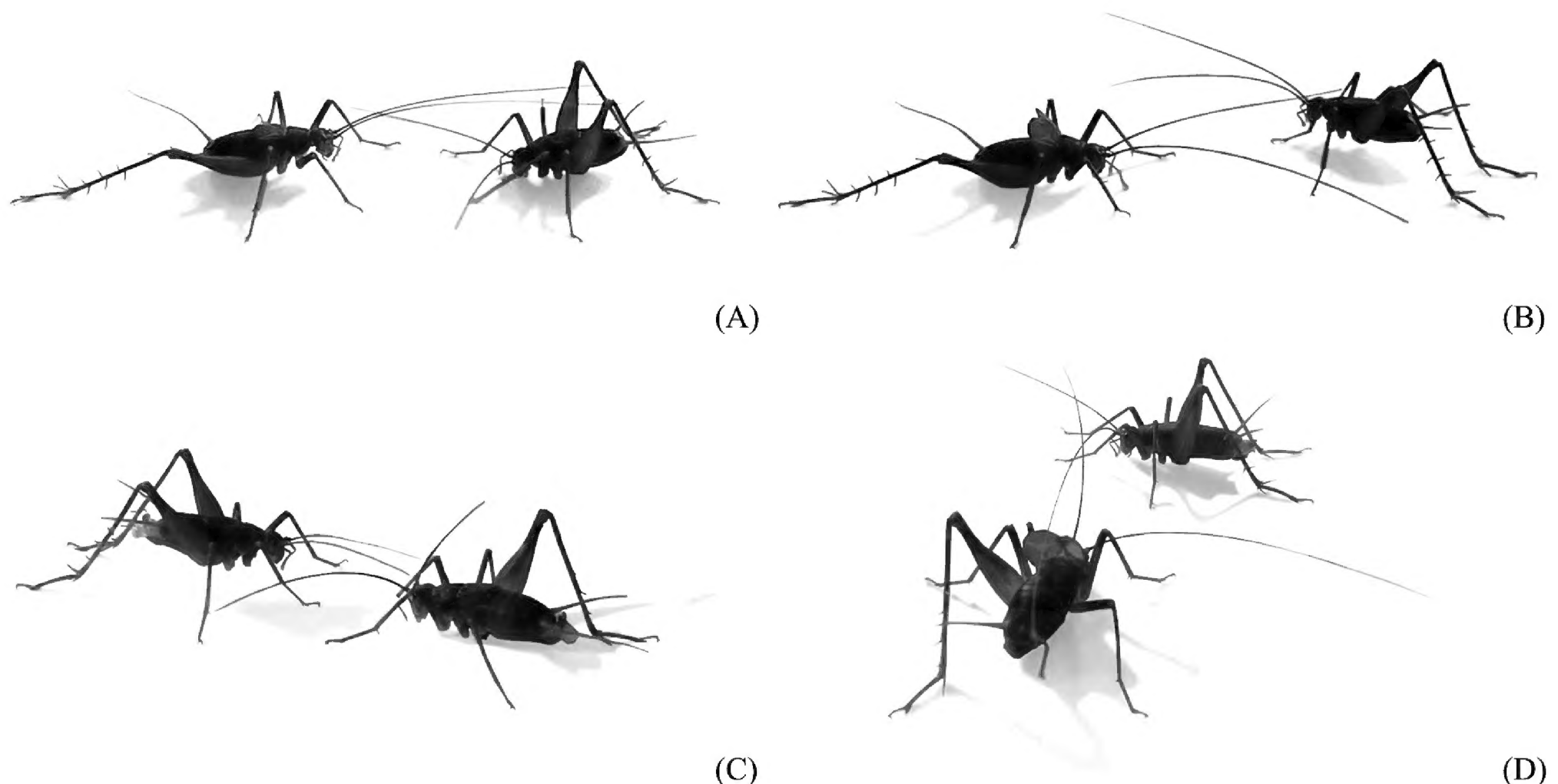


Fig. 1. Male-male interactions of *Endecous chape*. A. Antennation in face-to-face position; B. One male stridulating while the other lifts up his body; C. Same-sex sexual behavior, with both males producing a spermatophore; D. Male in the center of arena lifting up his body and stridulating, while the other moves to the corner.

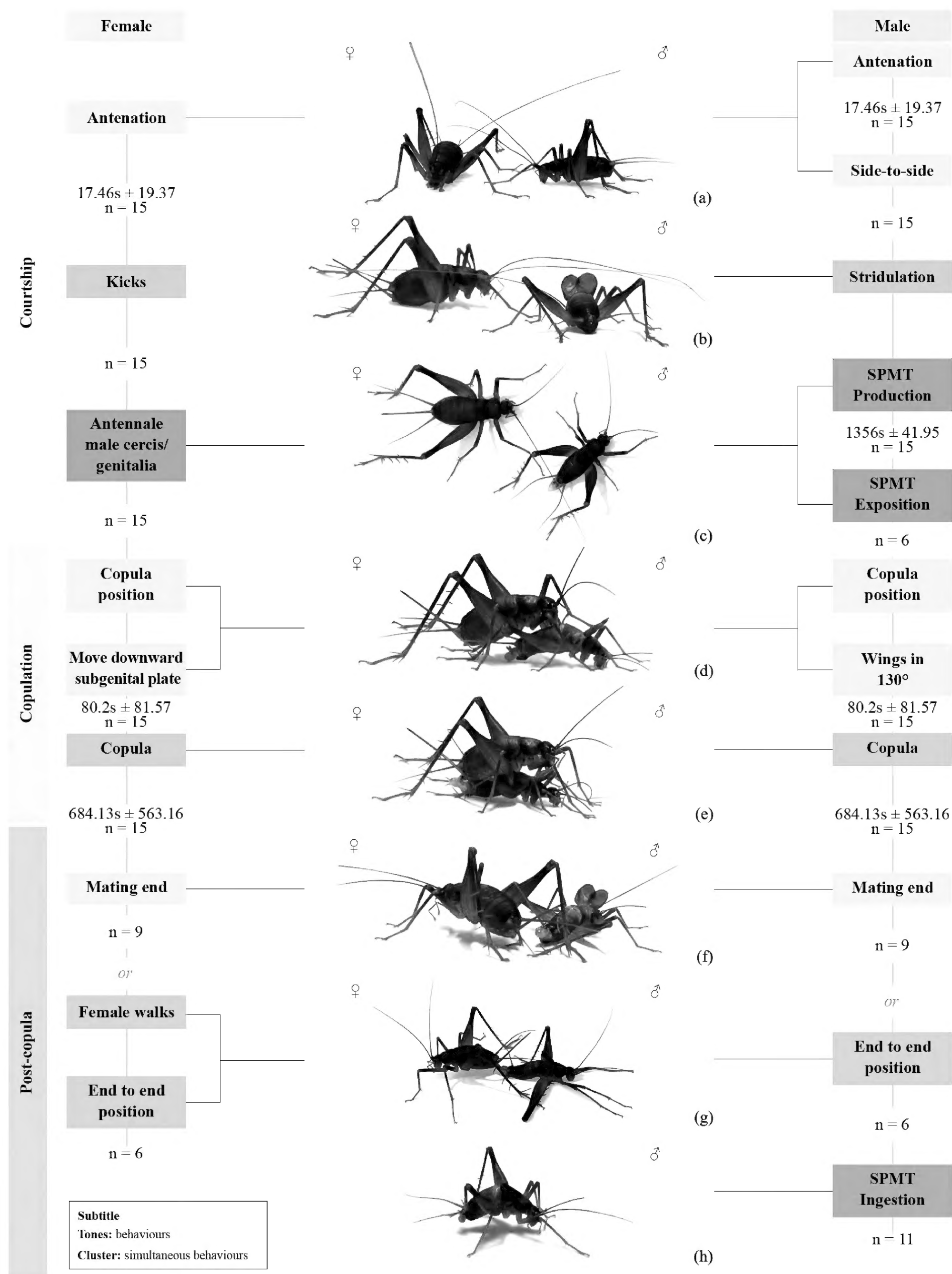


Fig. 2. *Endecous chape* mating behavior. A. Courtship position; B. Male stridulating next to the female; C. Exposure of the spermatophore; D. Copulation position; E. Copulation; F. End of copulation; G. Female dragging the male in end-to-end position; H. Male removing the spermatophore.

of sudden but mild anteroposterior vibrations with his body and touched the female's abdomen, cerci, and hind femora with his hind tarsus. Males also moved their cerci up and down and slightly lifted the abdomen. During the courtship stridulation, six males partially everted their genitalia and slowly positioned themselves to show their backs to the female, exposing the spermatophore (Fig. 2C). Nine males exposed the spermatophore when they were in the mating position. The time between spermatophore production (since genitalia exposition) and complete exposition was $1356 \text{ s} \pm 41.95$ ($1296 - 1402 \text{ s}$, $n = 15$). Males stopped emitting acoustic signals when they assumed the mating position.

Females touched male cerci and abdomen with their mouthparts or antennae regardless of whether or not the male had exposed the spermatophore. Then males walked backwards with the abdomen touching the substrate, raising their tegmina about 130° to the horizontal body axis, positioning himself underneath the female and assuming the copulation position (Fig. 2D). After assuming this position, the mean time for mating to start was $80.2 \text{ s} \pm 81.57$ ($12 - 304 \text{ s}$, $n = 15$). During the copulation positioning, females moved their subgenital plates downwards and males engaged their phallic complex (pseudoepiphallus) with the females' genitalia. During copulation (Fig. 2E), males performed upward and lateral movements of the cerci. Eight females moved away spontaneously from the copulation position while males remained attached, deterring the female's escape. Mating ended when females detached from males, assuming no specific position (Fig. 2F). In six observations, females walked or jumped and assumed an end-to-end position, dragging males (Fig. 2G). In these cases, females freed themselves from males using their hindlegs.

Copulation duration was $684.13 \text{ s} \pm 563.16$ ($182 - 2276 \text{ s}$, $n = 15$). The elapsed mating time between sexual recognition by antennation to couple separation was $1072.86 \text{ s} \pm 717.10$ ($194 - 2837 \text{ s}$, $n = 15$).

After the couple separated, males retained the spermatophore and removed it using their hind tibial spines (Fig. 2H); three males tried to remove it with mandibles, bending their bodies, without success. After spermatophore removal, the male ate it ($n = 11$) or left the spermatophore on the substrate ($n = 3$). One male retracted his genitalia along with the spermatophore. Post-copulation songs were emitted by seven males right after the couple separated. In two observations, males began another courtship, stridulating and producing another spermatophore. Those cases were observed for 50 min, and the females were not receptive, so subsequent matings were not observed.

Oviposition behavior.—When released in the arena with wet sand substrate, females stayed still for $77.21 \text{ s} \pm 16.36$ ($42 - 112 \text{ s}$, $n = 15$). Afterwards, they started to walk through the arena touching the substrate with antennae, maxillary, and labial palpi, also ingesting substrate particles. Then one female lifted her body with her hindlegs and positioned her ovipositor 40° in relation to the substrate (Fig. 3A). Females that displayed oviposition behavior pressed their ovipositor tips against the sand surface and walked backwards to penetrate the substrate. Afterward, they lifted their bodies up and down, always redirecting their ovipositor at another angle (not exceeding 75°) (Fig. 3B), and repeatedly penetrated the substrate. Finally, they buried their ovipositors until the subgenital plate contacted the substrate (Fig. 3C).

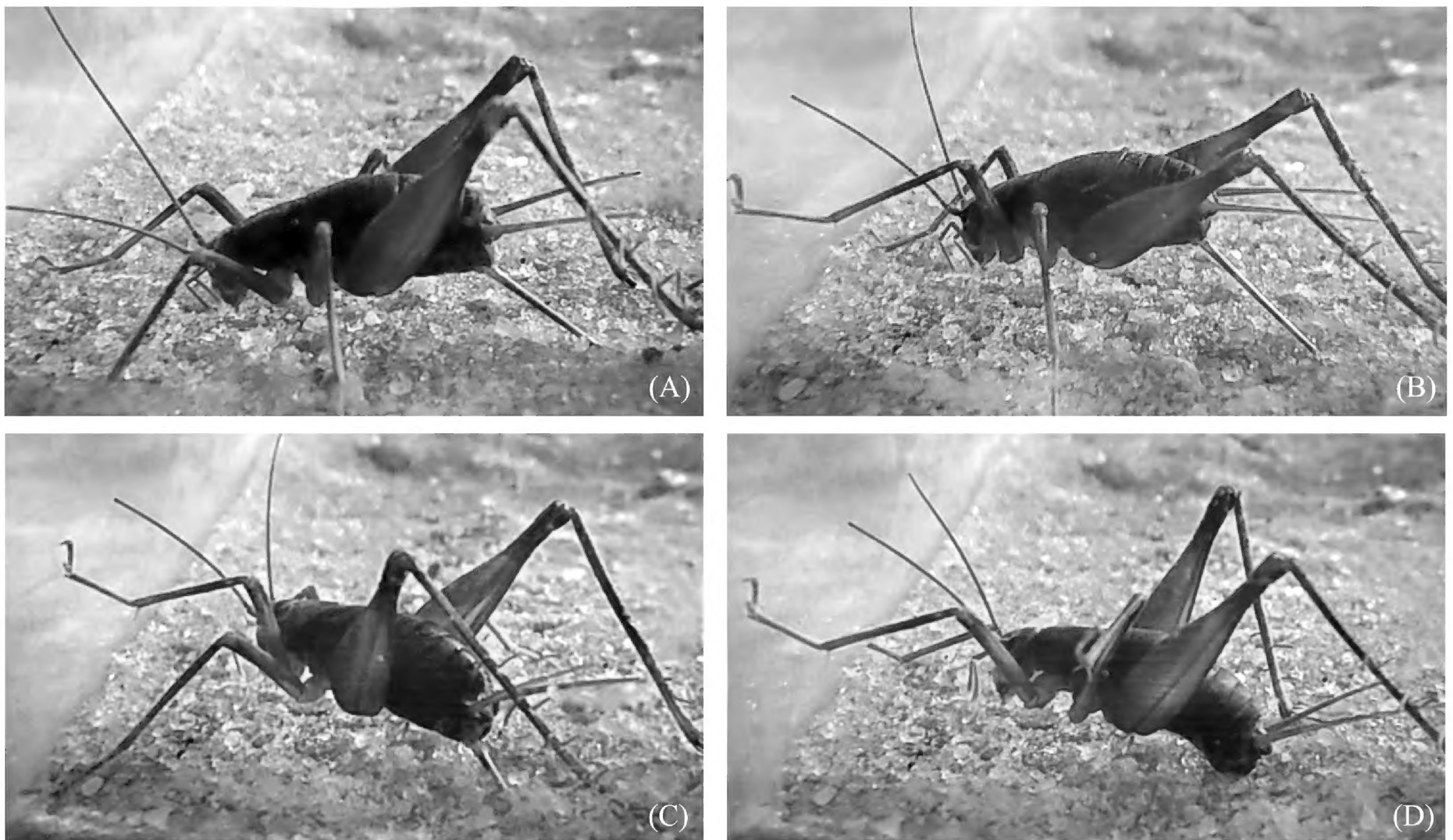


Fig. 3. *Endecous chape* oviposition behaviors. A. Female pressing the tip of ovipositor against the sand surface at a 40° angle; B. Female redirecting the ovipositor at another angle (about 70°); C. Female burying the ovipositor; D. Female with the ovipositor penetrated, remaining immobile.

When the ovipositor penetrated the substrate, females remained motionless for 295.43 ± 26.86 (245 – 362 s, $n = 15$; Fig. 3D) and then slightly lifted the abdomen tip. After this behavior, we observed that eggs passed through the ovipositor's valves. During egg laying, females partially lifted the ovipositor with subsequent penetration. The re-penetration occurred several times with the ovipositor always deflected at another angle. The oviposition behavior lasted 2340 ± 441 (1632 – 2938 s, $n = 15$). In total, 1235 eggs were oviposited, with each female laying 88 ± 20 (45 – 156, $n = 15$) eggs.

Discussion

Antennal contact.—The antennal contact observed in *E. chape* prior to agonistic and mating behavior has been reported in previous studies (Alexander and Otte 1967, Boake 1984, de Mello and dos Reis 1994, Prado 2006). This is a crucial behavior that allows intraspecific, sexual, and age profile recognition between individuals (Rence and Loher 1977, Tregenza and Wedell 1997). Thus, antennal contact is an important driver of reproductive behaviors and has been reported for all cricket species studied to date. Agonistic, courtship, or other reproductive processes do not start before antennal contact (Alexander and Otte 1967). Those interactions were preceded by grooming in *E. chape*, probably allowing the removal of substances that may obstruct olfactory sensilla, impregnating such parts with contact pheromones to recognize partner fitness (Rence and Loher 1977, Balakrishnan and Pollack 1997, Tregenza and Wedell 1997, Böröczky et al. 2013, Sakura and Aonuma 2013).

Male-male interactions.—The male-male interactions of *E. chape* involve multiple levels, from antennation to agonistic interactions with reciprocal fights to same-sex sexual behavior. Different levels of aggressiveness are common for other cricket species (Alexander 1961), and are related to a male's fight performance (Rillich et al. 2007), based on age, size (Alexander 1961), or prior contacts (Adamo and Hoy 1995).

Similar male/male antennation and body lifting as those of *E. chape* were also described for *Eidmanacris corumbatai* (Prado 2006). These behaviors, along with body size and antennal lashing, as observed in *Phaeophilacris spectrum* (Dambach and Lichtenstein 1978), may be a visual clue for a male to decide to not fight, increasing his chances of survival, avoiding injury/damage, and saving energy (Parker 1974). The wide range of agonistic behaviors presented by *E. chape* indicate that crickets have elaborate systems to define dominance and subordination.

The same-sex sexual behavior of male *E. chape* may occur due to failure in sexual recognition (Bailey and Zuk 2009, Bailey and French 2012) that can occur through pheromones left by females during previous matings (Thomas and Simmons 2009), or because postures or motor patterns of males are similar to females, inducing male's courtship or copulation (Wendelken and Barth 1985).

Mating behavior.—After pair formation, males of *E. chape* interacted with the females through several channels of communication, including stridulation, body vibration, and antennation. Although those interactions are common in the communication system during cricket courtship (Alexander 1960, 1962), little is known about what type of message is transmitted to the female. In some cricket species, those signals can send information about the genetic quality of the male to the female (Gray and Cade 1999). The intensity of the emission of these signals by the male may be relat-

ed to the female's age and experience in low densities, i.e. younger females and/or females that have experienced low density tend to be more selective (Tinghitella 2014), requiring male displays that meet or exceed minimum requirements (Boake 1984) like body vibrating, spermatophore exhibition, and sound production.

Antennation in *E. chape* is different than that of *E. corumbatai* and the second copulation phase of *Nemoricantor maya*, in which the male whips his antennae without touching the female (Boake 1984, Prado 2006). In *E. chape*, antennation is identical to that of *Adelosgryllus rubricephalus* (Zefa et al. 2008), *Eidmanacris meridionalis* (personal observation), and the first copulation phase of *Nemoricantor maya* (Boake 1984), where males and females touch each other quickly. A lack of data for other species of Phalangopsidae does not allow further comparisons.

Body vibration promotes substrate waves (Bell 1980), which are perceived by the females through the subgenual organs (Alexander and Brown 1963) and can provide information about the adaptive value of males, quality of environments that they occupy, or the presence of predators (Alexander and Otte 1967, Dambach 1972, de Mello and dos Reis 1994, Lunichkin et al. 2016). However, these assumptions have not yet been tested. In a specific case, females of *Vanzoliniella sambophila* (Phalangopsidae) will only mate if the male drums the substrate with his forelegs, producing vibrations in dry leaf litter (de Mello and dos Reis 1994).

Exposition of the spermatophore may be associated with sexual selection, allowing females to evaluate male genetic qualities since large males tend to produce larger spermatophores (Sakaluk 1985), representing good nutritional status or mating effort associated with fertilization success (Wedell 1994). Furthermore, larger males generate more fertile daughters (Simmons 1987) and more competitive sons (Simons and Roff 1994). Larger spermatophores may benefit females and increase their fecundity, since they present more accessory substances capable of increasing prostaglandin levels in females, leading to higher rates of oviposition (Loher et al. 1981). However, this has not yet been tested for *Luzarinae* crickets, including *Endecous*.

For the Phalangopsidae species whose mating behavior has been described (except *Phaeophilacris bredoides* Kaltenbach, 1986 and *P. spectrum*), the spermatophore always remains with the male after copulation (Alexander and Otte 1967, Dambach and Lichtenstein 1978, Boake 1984, Gnaspini and Pelegatti-Franco 2002, Prado 2006, Zefa et al. 2008, Lunichkin et al. 2016). Phalangopsidae males removing the spermatophore with the hind tibial spines is reported here for the first time, since generally males bend their body and pick up the spermatophore with their mouthparts, as occurs in *Adelosgryllus rubricephalus* Mesa & Zefa, 2004 (Zefa et al. 2008), or rub the end of their abdomen against the substrate, as in *Nemoricantor maya* (Alexander and Otte 1967, Boake 1984) and *Strinatia brevipennis* Chopard, 1970 (Gnaspini and Pelegatti-Franco 2002). Males that ingest the spermatophores can use the nutrients to produce other spermatophores, allowing subsequent copulas (Zefa et al. 2008), but this hypothesis has not been tested yet. However, males of *E. chape* do not always eat the spermatophore. We hypothesize that due to the latency between the end of copulation to the beginning of the next one, there may be little selective pressure to reacquire nutrients.

In most Phalangopsidae species whose copulation behavior has been studied, the male inclines his tegmina over his head exposing the dorsal region of the thorax. In *Eidmanacris corumbatai* and *Endecous itatibensis* Rehn, 1918 this allows the female to access the metanotal gland opening. This opening secretes substances (nuptial gift) that are ingested by the female (Gnaspini and Pele-

gatti-Franco 2002, Prado 2006), probably giving the males additional time to transfer more sperm to the female copulatory papilla, and transferring nutrients to females that may indirectly benefit the offspring (Boggs 1995, Poiani 2006). On the other hand, the metanotal gland is not present in *E. chape*, *A. rubricephalus* (Zefa et al. 2008), *P. bredoides* (Lunichkin et al. 2016), *P. spectrum* (Dambach and Lichtenstein 1978), *V. sambophila* (de Mello and dos Reis 1994), *Pizacris zefai* (Mews & Sperber, 2010) (Souza-Dias et al. 2015), and *N. maya* (Alexander and Otte 1967, Boake 1984). In these cases, the inclined tegmina can act as support for the females to remain in the copula position, since they are much larger than the males. Alternatively, it may be a plesiomorphic behavior (Alexander and Otte 1967).

In some observations, females of *E. chape* tried to interrupt copulation early by forcing their hindlegs against male bodies or jumping, and the males in turn avoided the escape of the females perhaps due to the strong connection promoted by the phallic sclerites. This male strategy to prevent the female from escaping during copulation may occur in *E. chape* due to high competition for females, since the sex ratio is apparently very male-biased (Fianco M, 2018, unpublished data). In Luzarinae, male phallic claspers (pseudepiphallid parameres) used to hold the female copulatory papilla and keep the female attached during copulation are relatively common (de Mello 2007, Souza-Dias and Desutter-Grandcolas 2014, Souza-Dias et al. 2015, 2017). This type of behavior seems to be well adapted in *Aracamby* de Mello, 1992 (Phalangopsidae) whose males bear claspers in the paraprocts that grab the female during copulation, preventing her from aborting the copulation (de Mello 2007).

Oviposition behavior.—The fact that we did not observe oviposition when one or two females were in the arena may be related to the lack of adequate conditions and/or lack of correspondence to their natural environment, evidenced by the long time which females spent exploring the substrate. In addition, the observation time (60 min) may have restricted such observations, with females still combing the substrate searching for suitable locales for oviposition and not laying eggs during the observation period. Contrarily, we observed oviposition when three females were put together into the arena. Therefore, these individuals may have experienced the “group effect”, either as a numeric effect and/or synergistic inter-individual effect, as reported in vertebrates (Krams et al. 2009) and invertebrates (Salzemann and Plateaux 1988, Avilés and Tufiño 1998, Le Goff et al. 2010, Lihoreau and Rivault 2008). Another hypothesis is that *E. chape* is a gregarious cricket, meaning that it lives in larger groups, as reported by Boake (1984) for *N. maya*. The presence of more individuals might be related to defense against predation of both eggs and nymphs, as well as an increased rate of nymph development and the probability of offspring surviving to maturity. However, this has not yet been tested for crickets.

All oviposition behaviors presented by *E. chape* have been reported in other Gryllidae species (Destephano et al. 1982, Evans 1983, Sugawara 1993). Some behaviors, like females combing the substrate, may be interpreted as a search for an oviposition site that offers adequate temperature (Destephano et al. 1982) and moisture, as indicated by Boake (1984) with *N. maya*, and tested by Farias-Martins et al. (2017) with *Ubiquepuella telytokous* Fernandes, 2015 (Phalangopsidae), among other qualities that are important choices for offspring success. Similarly, numerous insertions of the ovipositor into the oviposition site may be a method for preparing the oviposition site or a way to lay more eggs, which both ensure greater reproductive success.

Conclusion

Most of the behaviors observed in other Phalangopsidae species during reproductive encounters were also observed in *E. chape*. The behavioral sequences that we observed and quantified show a rich diversity in the reproductive behaviors of both males and females, as well as diverse communication channels. Studies like this are important for a better understanding of the evolution of Grylloidea behaviors, especially Phalangopsidae, from both a phylogenetic and a behavioral-evolutionary perspective. In addition, these features may be useful in distinguishing cryptic species and are models for future sexual selection studies.

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